

# Reversible Epithelial Adhesion Closes the Mouth of *Beroë*, a Carnivorous Marine Jelly

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**Abstract.** We investigated how the ctenophore *Beroë*, a carnivore of the marine zooplankton, keeps its mouth shut to maintain a streamlined body shape during forward swimming in search of prey. In big-mouthed, thin-walled beroids we found that mouth closure requires neither muscular nor nervous activity. Instead, mouth adhesion is due to paired strips of adhesive epithelial cells on opposing stomodaeal walls. The two joined epithelial layers make numerous close appositions interrupted by vacuolar intercellular spaces. At regions of apposition, the plasma membranes are highly folded and interdigitated with each other, and are separated by a uniform distance of about 15 nm. A dense cytoplasmic coat underlies the membranes at such appositions. Synapses of neurites are found on the basal ends of the adhesive cells. We found two orthogonally different orientations of the stomodaeal adhesive strips in *B. sp. vs. B. forskali*, correlated with different distributions of feeding macrocilia inside the stomodaeum.

Mouth opening in response to food requires muscular contractions of the lips. However, the stomodaeal adhesive strips are not pulled apart all at once, but are peeled apart starting from a site of vigorous muscular tension. The mouth re-seals after feeding, or after being experimentally pulled open, showing that tissue adhesion is functionally reversible.

Epithelial adhesion in *Beroë* appears to be a useful method for closing the mouth and streamlining the body of a gelatinous predator that spends most of its time swimming mouth-forward in search of prey. Opening of the mouth appears to be an efficient process as well, because peeling apart of the adhesive strips requires a smaller applied force than does separating them all at once. Tissue

adhesion in *Beroë* shares many structural and functional properties with transient adhesions formed between moving cells in embryos and in culture, and may be a useful experimental system for studying the mechanisms and regulation of dynamic cell adhesions.

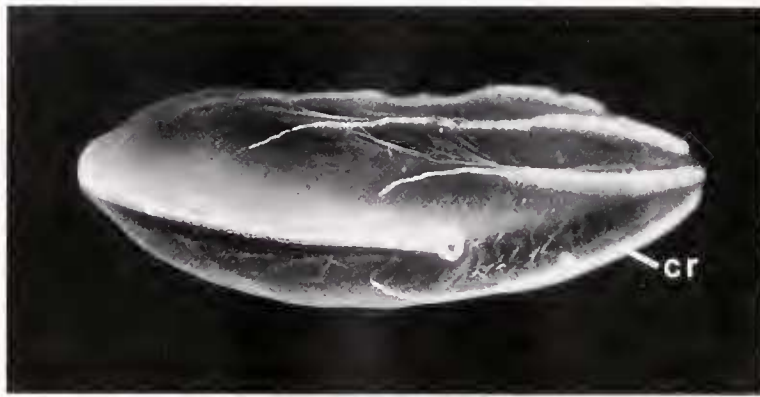
“Loose lips  
Sink ships.”

—U. S. Navy slogan, WW II

## Introduction

Ctenophores are important members of the gelatinous marine zooplankton and are significant predators in planktonic food chains (Thorson, 1971). Beroid ctenophores have a large mouth and a voluminous stomodaeum occupying most of the body, and are voracious predators of other ctenophores (Swanberg, 1974; Harbison *et al.*, 1978). *Beroë* actively seeks prey by swimming mouth forward, powered by the beating of giant ciliary comb plates. Yet the mouth remains closed, with the body shape streamlined, until prey is encountered. Then the mouth opens rapidly and the stomodaeum expands to suck in the prey (Horridge, 1965a; Tamm, 1982). Alternatively, the lips may spread over the prey, using the saber-shaped macrocilia lining the stomodaeum to bite off pieces (Horridge, 1965a; Swanberg, 1974; Tamm, 1983).

We have investigated the mechanism whereby a swimming *Beroë* keeps its mouth shut. We have found that mouth closure in certain beroids is due to a functionally reversible type of adhesion between paired strips of epithelial cells on the stomodaeal walls. Muscular activity is not required to keep the mouth shut, but is necessary to open the mouth in response to food. The adhesive seal is not separated all at once, but is peeled apart starting at a site of muscular tension. The mouth of *Beroë* may be a



**Figure 1.** *Beroë mitrata* swimming mouth forward (to the left) with the lips closed into a wide curved slit. The body is flattened in the stomodaeal plane with a blunt front end and tapering rear. Longitudinal rows of ciliary swimming plates (cr, comb rows) extend from the aboral end toward the mouth. Photograph kindly provided by Dr. Claude Carré, Station Zoologique, Villefranche-sur-Mer, France. Natural size.

useful model for studying the mechanisms and control of reversible tissue adhesions, as well as the biomechanics of feeding behavior in soft-bodied marine animals.

### Materials and Methods

#### Animals

*Beroë* sp. was collected at Woods Hole, Massachusetts, in fall, 1990. This unidentified species is similar to *B. sp.* collected at Woods Hole in fall, 1985, after Hurricane Gloria (Tamm and Tamm, 1988). The comb rows of this beroid run on high ridges that project from the flattened body surface.

*B. forskali* was collected at Monterey Bay, California, by Freya Sommer of Monterey Bay Aquarium, and shipped to the Marine Biological Laboratory in Woods Hole.

#### Observations on living material

An isotonic  $MgCl_2$ -seawater mixture (6.75%  $MgCl_2$ : seawater = 1:1) was used to block nervous and muscular responses in whole animals or in dissected preparations.

Experimental observations on the stomodaeal adhesive strips of *B. sp.* or *B. forskali* were made under a Wild dissecting microscope and recorded with a Panasonic CCD video camera and GYYR model 2051 video recorder allowing still-field playback and analysis. Still-fields were photographed from a Sony video monitor with an Olympus OM-2N camera on Kodak Tech Pan film.

Mouth opening responses of whole animals pinned to Sylgard were induced by a suspension of fresh egg white in seawater (A. Maselli, pers. comm). Responses were recorded with a Nikon macrolens on a Panasonic CCD video camera using the procedures described above.

Tracings of selected video fields were made on matte acetate directly from a video monitor.

Differential interference contrast (DIC) images of living stomodaeal adhesive strips were made with Zeiss 16 $\times$  or 40 $\times$  objectives and recorded with an Olympus OM-2N camera on Kodak Tech Pan film by electronic flash.

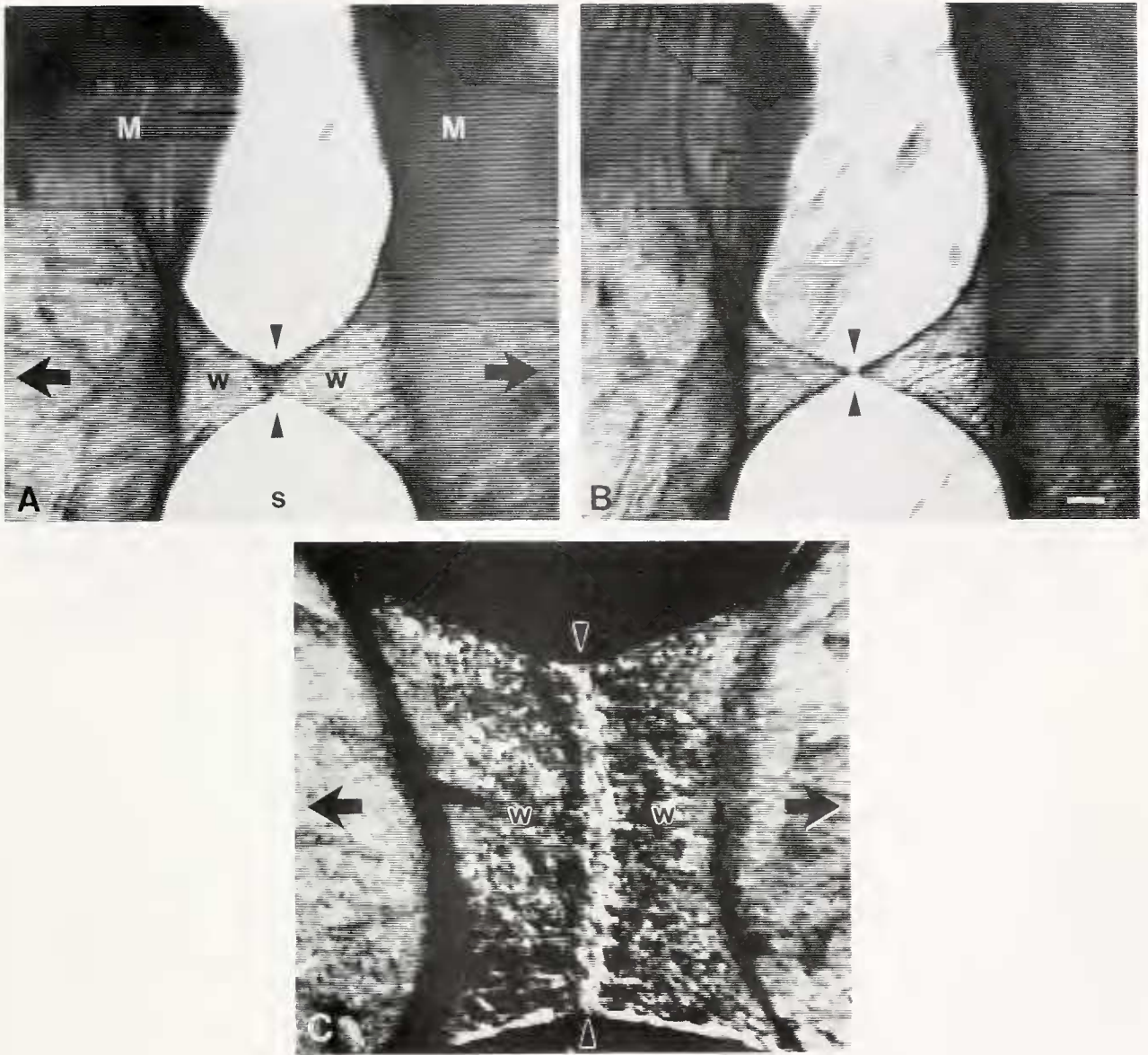
#### Electron microscopy

Closed mouths of *B. sp.* and *B. forskali* were fixed as follows. The animals were first relaxed in  $MgCl_2$ -seawater. Simultaneous glutaraldehyde-paraformaldehyde-osmium fixation was then performed and tissue was processed for electron microscopy as described previously (Tamm and Tamm, 1985).

### Results

Beroid ctenophores have a conical body flattened in the stomodaeal plane to varying degrees in different species. *Beroë* swims mouth forward at speeds of several cm/s or faster when seeking prey. In flattened thin-walled species such as *B. sp.*, *B. forskali*, and *B. mitrata*, the front end is wide and blunt with the lips closed into a long curved slit, and the body tapers towards the rear (Fig. 1). This streamlined body shape depends on the mouth remaining closed during forward swimming.

We examined how beroids with flattened streamlined bodies and thin flexible body walls (*i.e.*, *B. sp.* and *B. forskali*) keep their mouth shut while swimming. *B. sp.* and *B. forskali* differ dramatically from each other in the size and arrangement of their feeding macrocilia; as we will show, this difference in macrociliary patterns is correlated with orthogonally different orientations of mouth closure.

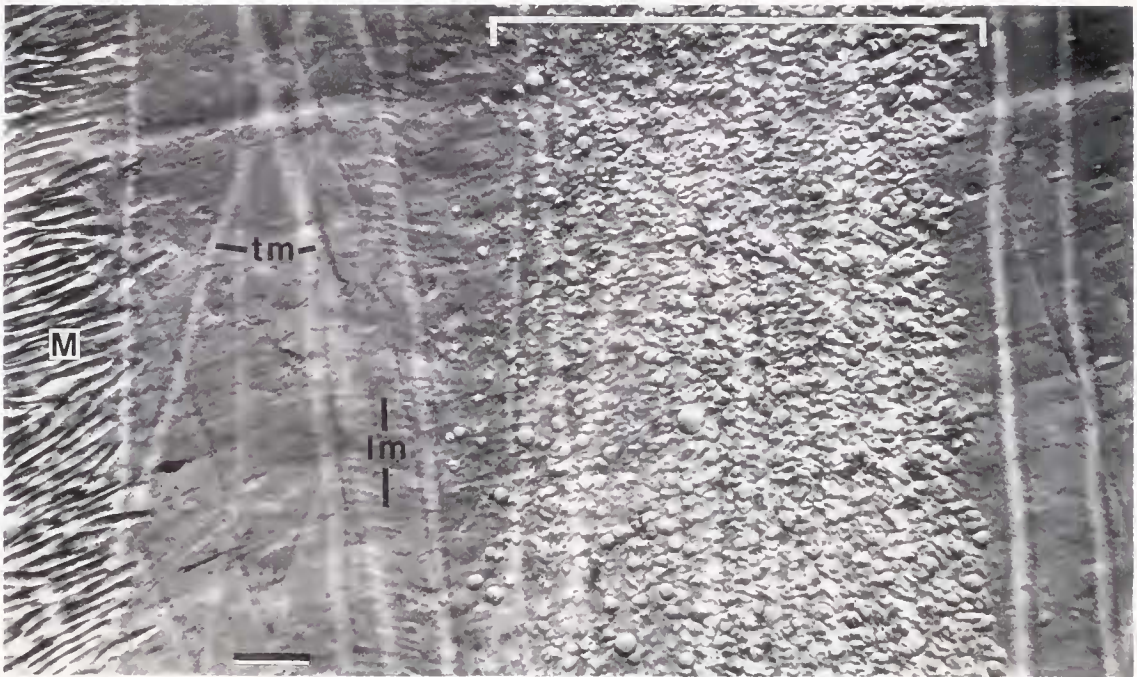


**Figure 2.** Zone of adhesion between Mg-relaxed lip segments of *Beroë* sp. under imposed tension (large arrows). A,B. The paired lip segments (left and right) are joined symmetrically along a zone (arrowheads) of stretched stomodaeal walls (w). The lip edges and furrowed macrociliary fields (M) are at the top; the stomodaeum (s) is down. Note that the attachment zone is located a short distance aboral to the macrociliary fields. B. Continued tension narrows the adhesive contact between the stretched lip surfaces (arrowheads). A short time later the lips snapped apart. C. Face view of the adhesion zone between stretched, separating stomodaeal walls (w) by darkfield microscopy. The adhesive contact runs medially (arrowheads) and scatters more light than the stretched surfaces. Scale bar: A,B, 165  $\mu\text{m}$ ; C, 110  $\mu\text{m}$ .

*First pattern of mouth adhesion: B. sp.*

Treatment of *B. sp.* with excess  $\text{MgCl}_2$  abolishes contraction of the body wall muscles and blocks neurally mediated ciliary responses (*i.e.*, ciliary inhibition). Mg-relaxed animals swim forward continuously with their mouth closed. The lips resist being pulled apart with forceps, as

if they were stuck shut. After being forcibly opened, however, the stomodaeal walls and mouth of  $\text{MgCl}_2$ -anaesthetized animals gradually close, and the lips re-seal within 10–15 min. Similar observations were made on dissected oral ends. These findings show that mouth closure is functionally reversible and requires neither muscular nor nervous activity to maintain or re-establish adhesion.



**Figure 3.** DIC view of the surface of a peeled apart lip of *Beroë* sp. in  $MgCl_2$ /seawater. The lip edge is to the left; the aboral direction is to the right. The adhesive strip (bracket) runs parallel to, and a short distance aboral to, the macrociliary field (M). The surface of the adhesive zone is covered with numerous small vesicles or craters. Subepithelial transverse muscle fibers (tm) run vertically and appear out-of-focus. The finer and more closely spaced longitudinal muscles (lm, cf. Fig. 5) run horizontally and are visible in the area between the adhesive strip and the macrocilia. Scale bar, 30  $\mu m$ .

The adhesive region in the mouth was located by examining segments of adherent lips excised from Mg-relaxed animals. We found that lip segments are fastened together along a narrow zone of the apposing stomodaeal walls (Fig. 2). The belt of tissue adhesion runs around the inside of the mouth, a short distance aboral to the band of macrocilia encircling the lip edge (Fig. 2). Therefore, mouth closure is not due to Velcro-like attachment of macrocilia on apposing lips, a possibility that initially had seemed likely to us.

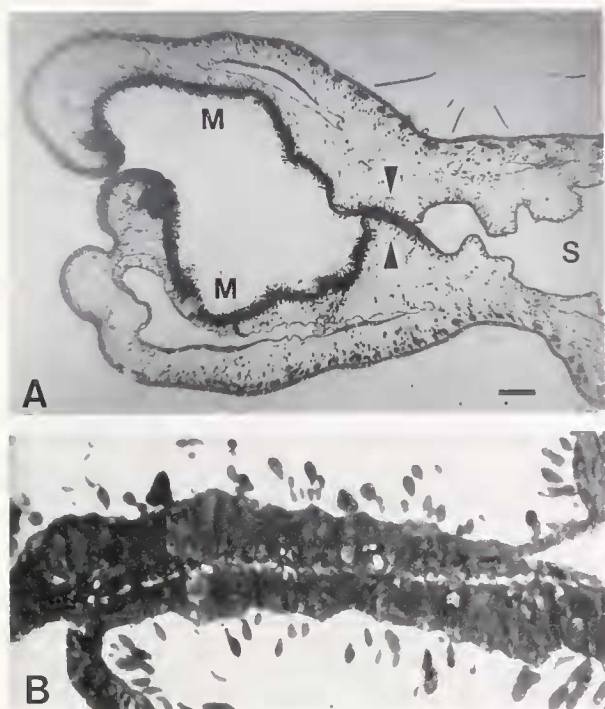
We next investigated the adhesive properties of closed lips. Adherent lip segments were pulled apart by forceps, starting at one end of the joined pair. Tension initially stretches the joined stomodaeal walls without separating the adhesive zone (Fig. 2A). Increased tension further draws out the two attached surfaces, which appear as mirror images of each other (Fig. 2B,C). Then the adhesive strips on either side separate at the site of greatest tension and the lips peel apart. This is followed by elastic recovery and flattening of the stretched stomodaeal walls.

Darkfield microscopy of joined, stretched lips under tension shows that the zone of stomodaeal contact scatters more light, and thus appears brighter than the adjacent walls (Fig. 2C). The increased light scattering is correlated with the greatly elaborated surface area of the adhesive cells (see below).

By DIC light microscopy the surface of mechanically peeled apart lips displays a well-defined tract of densely packed vesicles or vacuoles, that coincides with the location of the adhesive strips (Fig. 3). These vesicles or vacuoles are 2–10  $\mu m$  in diameter, and appear to be modifications of the apical surfaces of stomodaeal epithelial cells. The tract is 200–300  $\mu m$  wide and runs about 150  $\mu m$  aboral to the band of macrocilia. The stomodaeal surface on either side of the adhesive tract is relatively smooth and featureless.

Toluidine blue-stained thick sections through fixed, closed mouths show that the stomodaeal epithelium is markedly thicker in the adhesive strips, due to the increased height of cells in this region (Fig. 4). Even by light microscopy, it is evident that the two epithelial layers make numerous close contacts, interrupted by many vacuolar intercellular spaces (Fig. 4B).

Corresponding electron micrographs through adherent epithelial strips show that apposed cell surfaces are folded and interdigitated with each other (Figs. 5, 6). In such appositions, the two plasma membranes conform to each other and run parallel, separated by a uniform space of about 15 nm (Fig. 6). The intercellular space frequently contains dense amorphous material, but there is no obvious structural continuity between the apposed cell surfaces (Fig. 6). The cytoplasmic sides of the membranes



**Figure 4.** Toluidine blue-stained longitudinal thick sections ( $0.5\ \mu\text{m}$ ) through a closed mouth of *Beroë* sp. A, Survey view, lip edges at left. The stomodaeal walls are joined together by paired strips (here cut transversely) of thickened epithelia (arrowheads) located aboral to the macrociliary fields (M). S, Stomodaeum. B, Higher magnification of thickened joined epithelial strips. Apposing cell surfaces make numerous close contacts interrupted by vacuolar spaces. Scale bar, A,  $100\ \mu\text{m}$ ; B,  $17\ \mu\text{m}$ .

are coated with dense material and wispy filaments that run parallel to the membrane. These close appositions are found almost exclusively between plasma membranes of adhesive cells, being rare or absent between cells within either epithelial layer.

The regions of close apposition alternate with widely separated, vacuolar spaces between the epithelial surfaces (Fig. 5). The plasma membranes in the widely spaced regions do not bear dense cytoplasmic coats, and so are readily distinguishable from closely apposed membranes. The widely spaced regions seen in sections may correspond to the edges or rims of the round vesicles or vacuoles, seen by DIC on the surfaces of adhesive strips pulled apart by forceps (Fig. 3).

Numerous thin muscle fibers run parallel to one another between the basal ends of the adhesive cells next to the mesoglea (Fig. 5). These muscles extend in the longitudinal direction of the body for long distances under the entire stomodaeal epithelium, and are not restricted to the adhesive strips. Neuromuscular junctions are common and show the characteristic presynaptic triad structure of ctenophore synapses described by Hernandez-Nicaise (1973).

Synapses of neurites are also found on the basal ends of the adhesive cells, indicating that some function of the adhesive cells must be under nervous control. The possibility that cell-cell appositions may be neurally regulated is discussed below.

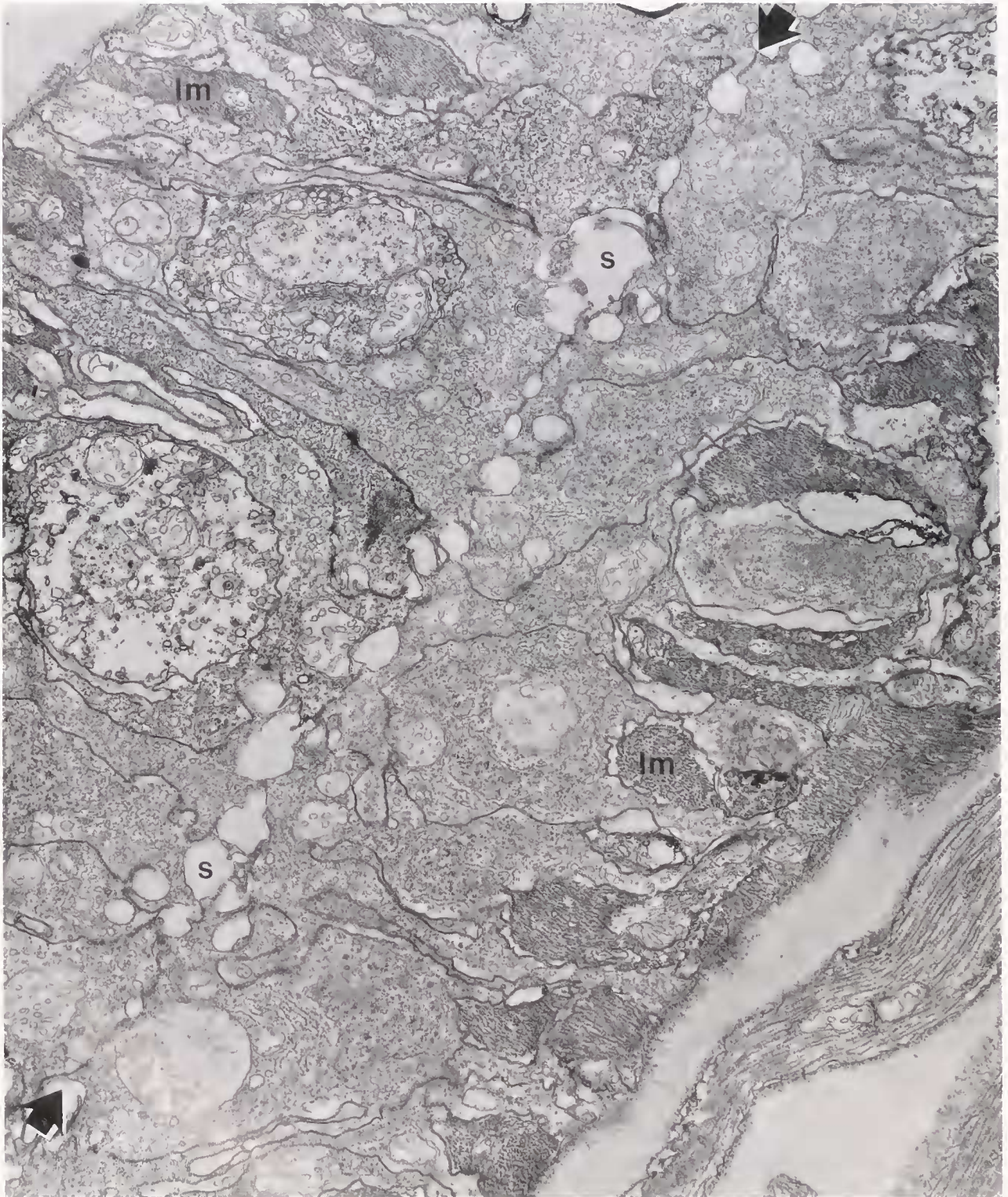
The stomodaeal adhesive strips also contain cells bearing actin pegs and onion-root cilia. Such cells are found in the epidermis of many ctenophores (Horridge, 1965b; Hernandez-Nicaise, 1974; Tamm and Tamm, 1991), and are thought to function as chemo- and mechanoreceptors (see Tamm and Tamm, 1991). In closed mouths, the actin pegs project into the vacuolar intercellular spaces between apposed epithelial layers. The cells bearing actin pegs and onion-root cilia synapse directly onto underlying longitudinal muscle fibers, suggesting a pathway for sensory control of stomodaeal muscles in response to food (see also below).

Glandular cells are abundant throughout the stomodaeal epithelium, including the adhesive strips. Large membrane-bound secretory droplets are packed into oval groups, many of which are larger than the cell nucleus. The secretory granules contain finely granular material, or coalesce and appear electron-lucent with coarse dense deposits and fibrils. These gland cells are similar to the spumous gland cells described in the epidermis of various ctenophores by Hernandez-Nicaise and colleagues (Hernandez-Nicaise, 1991).

The adherent epithelial layers are structurally identical and have a mirror-image symmetry about the plane of apposition. This suggests that each epithelial strip of the pair makes an equal contribution to adhesion, and that both surfaces are necessary for adhesion. In fact, the epithelial strip of an excised lip segment will adhere to an unmodified region of the stomodaeal wall, but such heterophilic attachments are weaker than adhesion between two lips.

#### *Mouth opening*

We investigated how *Beroë* separates its stomodaeal adhesive strips to open its mouth so widely and rapidly upon contact with food. Egg white pipetted onto the closed mouth of a *Beroë* pinned in seawater first triggers a series of brief, local muscular contractions of the lips perpendicular to the adhesive seal. These muscular twitches occur at various locations along the mouth edge, until one contraction pulls apart the adhesive strips at that site (Fig. 7A, B). The strips then rapidly peel apart from this point by coordinated muscular activity of the lips, leading to opening of the entire mouth (Fig. 7C–E). Without repeated stimulation, the mouth slowly relaxes and closes. Similar responses to egg white were observed in dissected oral ends.  $\text{MgCl}_2$ -relaxed animals cannot open their mouths due to inhibition of muscular and nervous activity.



**Figure 5.** Survey electron micrograph of adherent epithelial layers in a closed mouth of *Beroë* sp. The zone of adhesion runs diagonally from lower left to upper right (arrows), and consists of numerous close appositions of the cell surfaces alternating with vacuolar intercellular spaces (s). The plasma membranes have a cytoplasmic coat and appear darker at the contact regions (see Fig. 6). Thin longitudinal muscle fibers (lm) abutting the mesoglea are cut transversely.  $\times 9300$ .



**Figure 6.** Appositions of plasma membranes of adherent stomodaeal epithelial cells in a closed mouth of *Beroë* sp. Although folded, the apposed plasma membranes run parallel to each other and are separated by a distance of about 15 nm. Note flocculent material in the intercellular space. The cytoplasmic side of the membranes is coated with dense material. A,  $\times 108,400$ ; B,  $\times 93,400$ .

#### *Second pattern of mouth adhesion: B. forskali*

*B. forskali* and *B. mitrata* differ from other beroids in that they possess considerably larger macrocilia; more importantly for this study, their macrocilia are not restricted to a band around the inside of the lips, but cover a large area of the stomodaeal cavity. In *B. forskali*, the macrociliary field comprises longitudinal stripes that extend almost half the length of the stomodaeum (Figs. 8, 10).

Using transverse segments of the body of  $MgCl_2$ -relaxed *B. forskali*, we found that the flattened stomodaeal walls are joined by paired macrocilium-free ridges that run longitudinally down the midline of the stomodaeum, effectively dividing the stomodaeal cavity into two lateral pockets (Fig. 9). These adhesive strips begin near the lip edge and extend  $\frac{2}{3}$ – $\frac{3}{4}$  the length of the stomodaeal cavity (Figs. 8, 10).

Pulling the flattened sides of the stomodaeum apart with forceps shows that the paired longitudinal ridges of *B. forskali* possess adhesive and tensile properties similar to those of the circumoral adhesive strips of *B. sp.* In addition, light and electron microscopy reveals no morphological differences between the adhesive strips of *B. forskali* vs. *B. sp.* We have not yet made observations on how *B. forskali* or *B. mitrata* open their mouths to feed.

In *B. mitrata*, the macrociliary field covers the entire oral half of the stomodaeal cavity, except for two bare zones that extend longitudinally and medially through the macrociliary fields on either wall of the stomodaeum. Although we have no data at present to show that these macrocilium-free zones are adhesive and keep the wide mouth closed, their location suggests that they do so in a manner similar to the longitudinal adhesive strips of *B. forskali*.

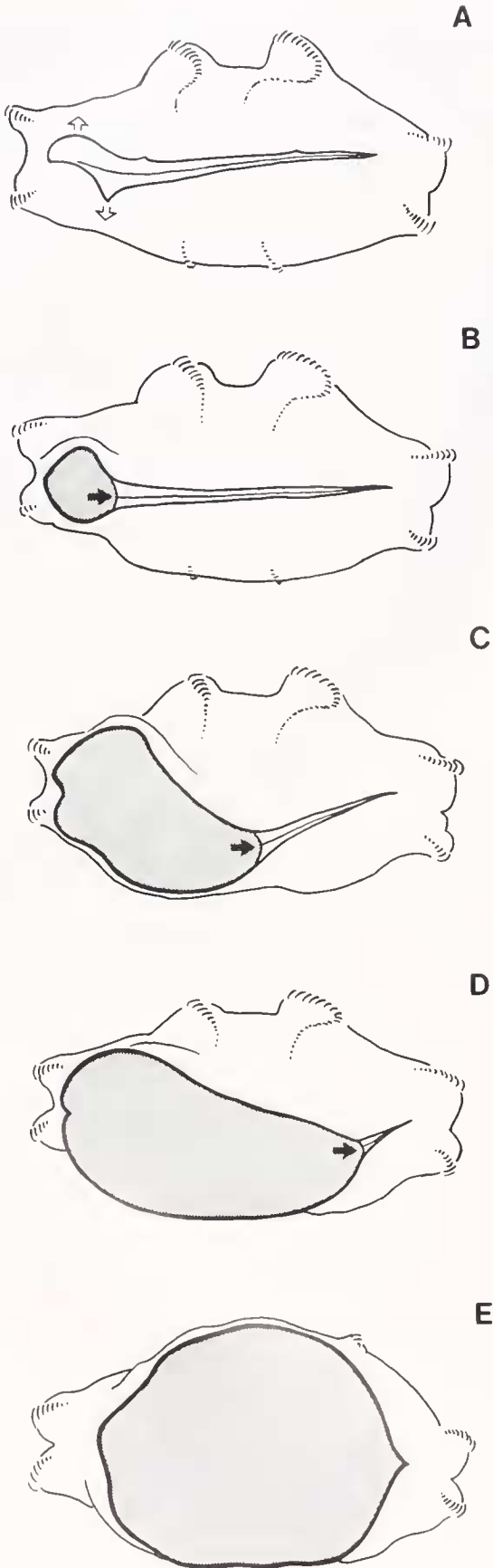
### Discussion

Our curiosity about how a swimming *Beroë* keeps its mouth shut led to the discovery of a novel, reversible type of tissue adhesion. We found that the stomodaeum is fastened together by a matched pair of apposed epithelial strips. The remarkable, and obviously necessary feature of this tissue adhesion is its functional reversibility: tissue bonding is rapidly broken when *Beroë* opens its mouth to ingest prey, and is readily reformed after feeding.

#### *Mechanism of adhesion*

The reversible appositions of stomodaeal adhesive cells in *Beroë* are similar in several respects to the transient adhesions formed between moving cells in embryos and in culture (Trinkaus, 1984). In both cases, apposed plasma membranes typically (1) are highly folded and interdigitated, (2) conform to each other and run parallel over broad areas, (3) are separated by a distance of 10–20 nm, and (4) show no obvious structural continuity between them. These features are in marked contrast to the standard types of structurally differentiated localized contacts found between cells, such as tight junctions, gap junctions, desmosomes, etc.

Because the apposed cell membranes of *Beroë* adhesive cells and moving cells in embryos and culture are not structurally bound to one another, "bonds between the cell surfaces in such appositions would be more readily



**Figure 8.** Surface at the oral end of one of the two stomodaeal walls of *B. forskali* (darkfield). The curved lip edge is at the top of the figure. Macroclia appear brighter and extend downward from the lip edge as tapering longitudinal stripes (s). The adhesive strip runs longitudinally along the midline of the stomodaeal wall (arrowheads). Scale bar, 2.3 mm.

made and broken and remade again than in junctions” (Trinkaus, 1984, p 171). These cell-cell appositions in fibroblasts are believed to be “a prime candidate for the kind of adhesion that moving cells require” (Trinkaus, 1984, p 171). Similarly, such appositions would seem well-designed for the reversible type of tissue adhesion required to seal *Beroë*’s mouth.

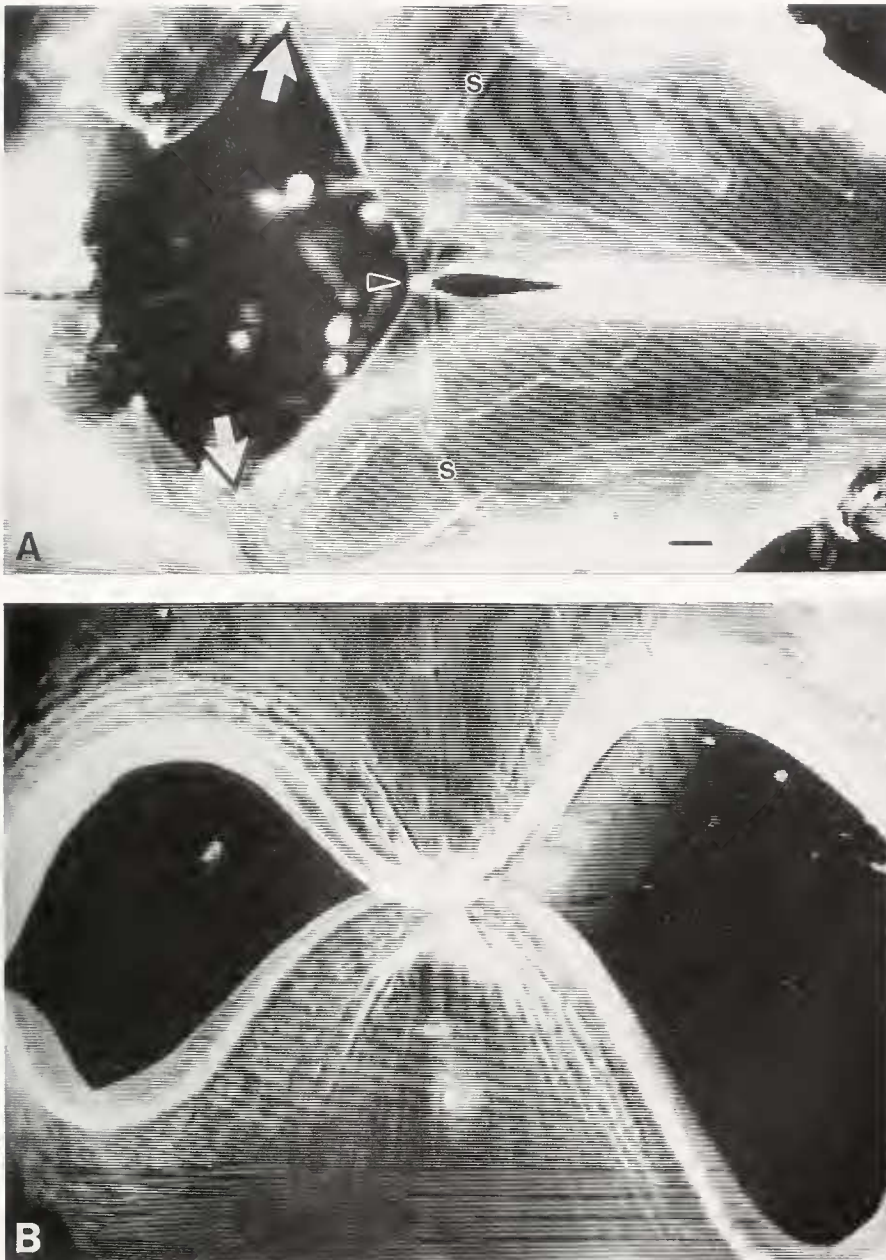
The physical or chemical mechanisms of such cell-cell adhesions are not well understood in any system (Trinkaus, 1984). Suggested mechanisms range from non-specific molecular attraction, such as London-van der Waals forces (Nachtigall, 1974; Trinkaus, 1984), to chemical bonding by molecular “glues” or specific cell adhesion molecules (Takeichi, 1990, 1991; Edelman and Crossin, 1991).

#### *Mouth opening and possible regulation of tissue adhesion*

Using egg-white as a feeding stimulus to induce mouth opening, we found that the mouth does not open all at once, as assumed previously (Tamm, 1982), but is peeled apart starting at a site of vigorous muscular tension on

**Figure 7.** Mouth opening of *Beroë* sp. induced by egg white (viewed orally). A, Local muscular twitches pull the left sides of both lips away from the adhesion zone (line inside the lips). B, Muscular tension separates the adhesive zone (arrow) and pulls open the lips on the left side of the mouth. C, Continued muscular activity peels apart the adhesive seal from left to right (2 s later). D, Peeling apart of the adhesion zone and opening of the mouth has almost reached the right side (3.5 s later). E, The mouth is fully open and gaping (6.5 s later). 3× natural size. Tracings of video fields from monitor.

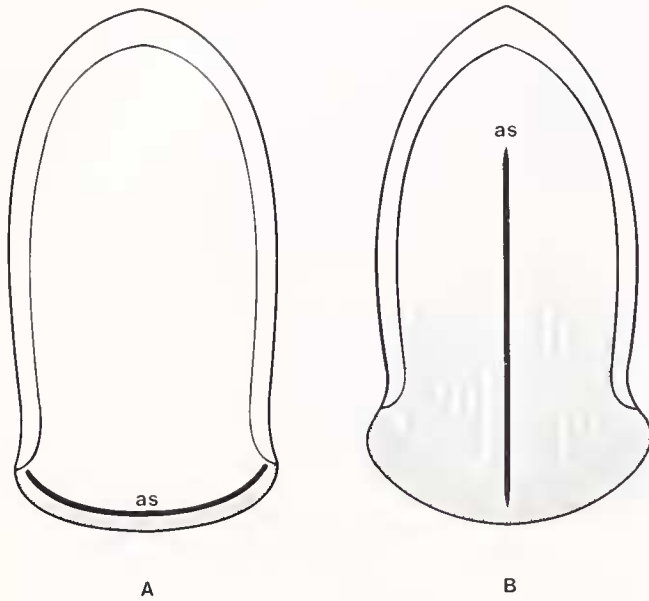




**Figure 9.** Stomodaeal walls of *Beroë forskali* are attached by paired longitudinal adhesive strips. A. The stomodaeal cavity of a transversely cut body segment is viewed along the oral-aboral axis from inside the animal. The stomodaeal walls on the left side have been cut and pulled apart (white arrows) to show the adhesive strips (s) running longitudinally on each wall. The strips are still joined like a spot weld at the arrowhead. The right side of the stomodaeum remains closed. B. Frontal view of a dissected mouth being pulled open with forceps. The middle of the mouth remains fastened by the longitudinal adhesive strips that divide the stomodaeal cavity into two lateral pockets. Scale bar: 1 mm.

the lips. Because peeling apart of two adherent surfaces requires a much smaller force, applied over a longer time, than pulling them apart all at once (Steinberg, 1964; Vogel, 1988), this method is likely to reduce the amount of muscular tension required to separate the stomodaeal adhesive strips of *Beroë*.

Mouth opening may also require concomitant changes in the adhesive properties of the epithelial cells themselves. The presence of synaptic contacts on the adhesive cells suggests that these cells make some kind of neuronally triggered effector response. Such responses may involve changes in the cortical cytoskeleton or cell



**Figure 10.** Diagram of mutually perpendicular orientations of stomodaeal adhesive strips (as, black bars) in *Beroë* sp. (A) vs. *B. forskali* (B). The inside of one wall of the flattened stomodaeum is shown. Macrociiliary fields are indicated by stipple. The number of longitudinal macrociiliary stripes in *B. forskali* (B) is reduced for clarity (see Fig. 8), and the relative width of the adhesive strips in both animals is exaggerated. Oral ends face down.

surface that modify the adhesive properties of the epithelial strips.

If so, mouth opening may require cellular de-adhesion processes as well as muscular activity. How might this be controlled? Mouth opening is triggered by contact of prey with sensory receptors on the lips. The presumed receptor cells bear actin pegs and onion-root cilia, and make synaptic contacts onto neurites of the nerve net (Hernandez-Nicaise, 1974; Tamm and Tamm, 1991). If this pathway is connected to muscles acting on the lips and also to cells of the adhesive strips, then food stimuli could signal both muscular contractions that pull the lips apart as well as de-adhesion of the epithelial cells themselves.

The gradual closure of the mouth after food-induced or experimentally forced opening does not require muscular activity. The voluminous extracellular matrix, or mesoglea, of ctenophores consists of a ground substance containing muscle fibers and other cells, as well as a felt-like meshwork of collagenous microfibrils linked to glycoproteins (Franc, 1985). Passive return of this fibrillar matrix to the resting state, following stress-evoked deformation, may be responsible for restoration of normal body shape that allows contact and adhesion of the epithelial strips on the two sides of the stomodaeum.

#### *Patterns of stomodaeal adhesive strips*

Beroëids can be divided into two main groups based on differences in macrociiliary size and distribution; these

patterns are believed to reflect differences in feeding behavior and prey type (Tamm and Tamm, 1990). In *B. sp.* and most other species, macrocilia are relatively small and are restricted to a narrow band around the margin of the lips. The adhesive strips in *B. sp.* also run around the lips, just inside the band of macrocilia.

In contrast, *B. forskali* and *B. mitrata* have larger macrocilia that cover a much greater area of the stomodaeal cavity. The adhesive strips in *B. forskali* run longitudinally along the midline of the stomodaeum, between the stripes of macrocilia. The mutually perpendicular orientation of stomodaeal adhesive strips in *B. sp.* and *B. forskali* is probably due to the different arrangements of macrocilia in the two species, because adhesion between the stomodaeal walls seems to require macrocilium-free zones of contact. We therefore predict that the paired macrocilium-free zones that run longitudinally through the wide macrociiliary fields of *B. mitrata* are also adhesive strips.

#### *Mouth closure in other beroëids*

Do all beroëids use epithelial adhesive strips to keep their mouths closed? Our preliminary observations on *B. cucumis* from Monterey Bay, California, suggest that this is not the case. *B. cucumis* differs from *B. sp.*, *B. forskali*, and *B. mitrata* in several respects: it is not appreciably compressed in the tentacular plane, but is round or oval in cross-section. Moreover, the body wall is markedly thicker and firmer, and the mouth is considerably smaller than those of the species described in this report. *B. cucumis* swims with its mouth closed or slightly ajar, but we have found by direct observation and dissection of living animals that neither the lips nor the stomodaeal walls are fastened together in any manner.

Evidently, the small oral opening and the relatively thick, rigid body wall of *B. cucumis* provide sufficient resistance to maintain normal body shape during forward swimming without the necessity of mouth closure mechanisms. Other beroëids with a similar body plan (*i.e.*, *B. ovata*) are likely to use the same strategy.

#### *Significance of stomodaeal adhesion*

At the moderate Reynolds number of a swimming *Beroë*, the streamlined body shape should be effective in reducing drag (Vogel, 1981). In thin-walled beroëids with stomodaeal adhesive strips, mouth closure does not require muscular or neural activity. Epithelial adhesion therefore seems to be a useful method for closing the mouth and streamlining the body of an active gelatinous predator that spends most of its time swimming mouth forward in search of prey. *Beroë* also appears to use an efficient method to open its mouth, because peeling apart the adhesive strips should require a smaller applied force

than pulling them apart all at once (Steinberg, 1964; Vogel, 1988).

From a comparative viewpoint, it is interesting that many hydrozoan polyps (but not other classes of Cnidaria) lack a permanent mouth; a mouth is created by muscular stretching and rupturing of the tissue in the oral region (Campbell, 1987). Breaching of the epithelia involves breaking of intercellular attachments (septate junctions). *Beroë*'s adhesive strips allow effective joining of the stomodaeal epithelium without obliterating the mouth, and muscular contractions are required to open it. In the simplest to the most complex metazoans, then, mouth opening is usually a motile process, but only in the most primitive cases does the mouth completely disappear when closed.

Finally, the epithelial adhesive strips of *Beroë* share many structural and functional properties with reversible adhesions formed between moving cells in embryos and tissue culture. The ctenophore system may provide unique experimental advantages for studying the mechanisms and cellular control of dynamic adhesions between cells and tissues.

#### Acknowledgments

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